

EVALUATION OF WOLF DENSITY ESTIMATION FROM RADIOTELEMETRY DATA

By


John W. Burch

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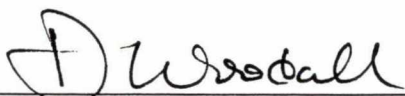


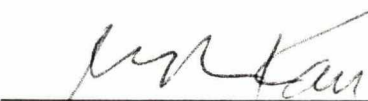



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EVALUATION OF WOLF DENSITY ESTIMATION FROM RADIOTELEMETRY
DATA

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By
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ABSTRACT

Density estimation of wolves (*Canis lupus*) requires a count of individuals and an estimate of area those individuals inhabit. With radiomarked wolves, the count is straightforward but estimation of area is more difficult and often given inadequate attention. The population area, based on the mosaic of pack territories, is influenced by sampling intensity similar to individual home ranges. If sampling intensity is low, population area will be underestimated and wolf density will be inflated. Using data from studies in Denali National Park and Preserve, I investigated these relationships using Monte Carlo simulation to evaluate effects of radiolocation effort and number of marked packs on density estimation. As the number of adjoining pack home ranges increase, fewer relocations are necessary to define a given percentage of population area. I evaluated the utility of nonlinear regression to adjust for biases associated with under sampling and present recommendations for monitoring wolves via radiotelemetry.

TABLE OF CONTENTS

| | |
|--|-----|
| Abstract..... | iii |
| Table of Contents..... | iv |
| List of Figures..... | v |
| List of Tables..... | vi |
| Acknowledgements..... | vii |
| Introduction..... | 1 |
| Study Area..... | 5 |
| Methods..... | 8 |
| Wolf density estimation..... | 9 |
| Comparison of two density estimation calculations..... | 12 |
| Evaluation of effects of radiolocation effort and number of packs..... | 13 |
| Estimating population area via nonlinear regression..... | 15 |
| Results..... | 17 |
| Density estimation..... | 22 |
| Effects of radiolocation effort and number of packs..... | 27 |
| Prediction of population area using nonlinear regression..... | 31 |
| Discussion..... | 31 |
| Management Implications..... | 37 |
| Literature Cited..... | 39 |
| Appendix A..... | 48 |

LIST OF FIGURES

| <u>Figure</u> | <u>Page</u> |
|--|-------------|
| 1. Location of Denali National Park and Preserve, Alaska..... | 6 |
| 2. Distribution of sample size of locations per pack per year for wolf packs in Denali.. | 19 |
| 3. Relationships between wolf home range size (HRS) and radiolocations/pack (LOCS) for (A) data accumulated over 1 year, and (B) data accumulated over 2 years..... | 21 |
| 4. Fall (A) and spring (B) wolf densities estimates, (wolves/1000 km ²) by year for 2 sampling intensities..... | 24 |
| 5. A comparison of fall and spring wolf densities for 1 year and 2 years of radiolocations. Each graph contrasts densities calculated in the standard way (DEN) to those standardized for radiolocation effort at the mean level over the entire study (MPSDen)..... | 26 |
| 6. Percent of wolf population area explained (A) and the coefficient of variation of the percent wolf population area explained (B) for sampling intensities at 0 to 150 locations per pack | 28 |
| 7. Thresholds of radiolocation effort at which an additional 5 locations per wolf pack would result in the specified (1-5%) increase in population area, based on Monte Carlo simulations of wolf telemetry data..... | 29 |
| 8. Fitted lines of predicted values comparing a curve quickly attaining an asymptote (A) vs. a line still increasing and not close to an asymptote (B)..... | 30 |

LIST OF TABLES

| <u>Table</u> | <u>Page</u> |
|---|-------------|
| 1. Pack sizes of radiomarked wolf packs in spring (S; approximately 15 March) and fall (F; approximately 1 October)..... | 11 |
| 2. Independent radiolocations obtained for each wolf pack each biological year (e.g. 87 = 1 May 1987 – 30 April 1988)..... | 18 |
| 3. Comparison of wolf densities (wolves/1,000km ²), mean locations per pack, and mean home range size calculated using 1 year of radiolocations vs. 2 years of radiolocations to determine population area, with mean pack size and number of packs used in the calculations..... | 20 |
| 4. Results of multiple regression to determine relationships between wolf density (wolves/1,000 km ²), mean pack size (MPS), and radiolocation effort, or mean locations per pack (MLOC), for density estimates based on 1 or 2 years of radiolocation data..... | 25 |

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INTRODUCTION

Estimates of wildlife abundance are cornerstones to understanding and managing wildlife populations. For wolves, abundance estimates are generally expressed as wolf density based on counts of wolves in a particular area and estimates of the size of that area (Mech 1973, Fritts and Mech 1981, Peterson et al. 1984, Messier 1985, Fuller 1989, Ballard et al. 1997). A recurring problem with most studies attempting to calculate wolf densities is a lack of sufficient radiolocations to produce reasonable estimates of the area wolves inhabit annually (National Research Council 1997).

Wolf density is often estimated from radiotelemetry data (Mech 1974, Van Ballenberghe et al. 1975, Messier and Crete 1985, Fuller and Snow 1988, Thurber and Peterson 1993, Mech et al. 1998). Other than variation in occurrence of lone non-territorial wolves (Fritts 1983, Van Ballenberghe 1983, Ballard et al. 1987, Mech 1987, Fuller 1989, Gese and Mech 1991), determining a count of wolves (the numerator of a density estimate) from radiomarked packs is relatively straightforward (Stephenson 1978, Peterson et al. 1984, Mech 1986, Fuller 1989, Hayes 1995). However, methods for calculating the population area (the denominator of a density estimate) are often subjective, and frequently are not thoroughly described. In contrast, Peterson et al. (1984) devoted an appendix on this subject for wolf density estimation on the Kenai Peninsula, Alaska.

Estimates of population area are based on the total area described by the mosaic of wolf territories as determined by radiotelemetry (Mech 1973, 1986; Peterson 1977; Ballard et

al. 1987; Fuller 1989). Most frequently, pack territories are determined by the minimum convex polygon (MCP) method (Mohr 1947, Odum and Kuenzler 1955), connecting the outermost locations into convex polygons, thereby defining the home range of individual packs (Peterson et al. 1984, Messier 1985, Mech 1986, Ballard et al. 1987, Fuller 1989, Hayes et al. 1991). Although many other home range estimators are available (Dixon and Chapman 1980, Anderson 1982, Bekoff and Mech 1984, Worton 1989, Boulanger and White 1990, White and Garrott 1990), and the MCP method is not without its theoretical shortcomings, as are all popular home range estimators (Boulanger and White 1990, White and Garrott 1990), the MCP method has been consistently employed for wolf density estimation (Peterson et al. 1984, Messier 1985, Mech 1986, Ballard et al. 1987, Fuller 1989, Hayes et al. 1991).

Once pack territories are determined, the population area is derived by calculating the area encompassed by the outer boundaries of the territorial mosaic. However, determining the population area requires making assumptions about the perimeter of the population area, extra-territorial forays or dispersals, territory overlap, and inclusion of areas between pack territories.

With the MCP method, home range size and therefore, population area size, is dependent on sampling intensity, and increases asymptotically as the number of radiolocations increases (Fritts and Mech 1981, Bekoff and Mech 1984, Swihart and Slade 1985, Ballard et al. 1987, Fuller and Snow 1988, White and Garrott 1990). Therefore,

estimates of wolf density are likely inflated when sampling effort is low because the size of the population area is underestimated. Sampling intensity has been explored for determining home range sizes for individual wolves or single packs (Fritts and Mech 1981; Bekoff and Mech 1984; Ballard et al. 1987, 1998; Fuller and Snow 1988) but not for a population.

The number of wolf packs monitored also influences estimation of population area. With a large number of packs, a large proportion of the population area can be estimated with only a few locations per pack, because wolves are generally territorial. As the number of instrumented packs decreases the proportion of the population area described at a given radiolocation sampling effort will also decline. Evaluation of the effects of pack sample size on density estimation may be important to compare annual wolf abundance estimates or to compare the results of different studies.

Fuller and Snow (1988) provided recommendations for estimating wolf densities with radiotelemetry data, based on their studies of a relatively dense wolf population in northern Minnesota. They suggested that 30–35 radiolocations per pack were sufficient for density estimation because an additional 5 locations resulted in < 5% increases in estimating individual home range sizes, and this sampling intensity was “enough to determine whether another wolf pack might reside between 2 territories.” They went on to recommend that areas “large enough to include a minimum of 4-5 wolf packs” were probably sufficient to estimate wolf density. They did not evaluate the interrelationships

of radiolocation intensity and the number of packs monitored on estimation of population area.

In some studies involving wolf density estimation, area-observation curves have been generated for individual wolves or single home ranges (Fritts and Mech 1981, Bekoff and Mech 1984, Ballard et. al. 1998) and classically, these curves are asymptotic, although this concept has been challenged (Gautestad and Mysterud 1995). This same method can also be applied to a group of adjacent home ranges, a population area.

Because of the asymptotic nature of area-observation curves (Odum and Kuenzler 1955), nonlinear regression (NLR) may be useful for estimating the 'true' population area (the asymptote of the regression function) when samples of radiolocations are few.

Theoretically, estimating the asymptote would account for biases resulting in underestimation of this parameter when using the conventional MCP method.

Furthermore, NLR would provide a measure of precision for the asymptote, and therefore the density estimate, assuming no uncertainty in the count of wolves.

Ongoing studies of wolves in Denali National Park and Preserve Alaska (Denali), provided an opportunity to evaluate wolf density estimation using radiotelemetry data. One objective of the Denali study was to biannually estimate wolf abundance in the park. This entailed monitoring ≤ 16 instrumented wolf packs per year, amassing over 5,000 wolf radiolocations during March 1986 – April 1996. Further, Denali wolves and their

prey occur at substantially lower densities (Mech et al. 1998) than those studied by Fuller and Snow (1988).

My objectives were to: 1) illustrate the influence of radiolocation effort on wolf density estimates by comparing results based on 1 year and 2 years of combined radiotelemetry data, 2) investigate the effects of the number of radiolocations and the number of packs on estimation of population area for wolf density calculations, 3) evaluate the utility of NLR for accounting for sampling bias in determining population area, and 4) provide recommendations for monitoring wolf abundance in low-density wolf populations where ever they may occur.

STUDY AREA

The study area primarily encompassed areas north of the Alaska Range within and adjacent to Denali National Park and Preserve (63° north latitude, 151° west longitude) (Fig. 1). Denali, formerly known as Mount McKinley National Park (6,900 km²), was established in 1917 primarily to protect its wildlife populations (National Park Service 1986). In 1974, Mount McKinley National Park was designated a Biosphere Reserve under the United Nations Man and the Biosphere Program. In December 1980, with passage of the Alaska National Interest Lands Conservation Act, Mount McKinley National Park was greatly expanded (to 24,400 km²) and renamed Denali National Park and Preserve (Denali).

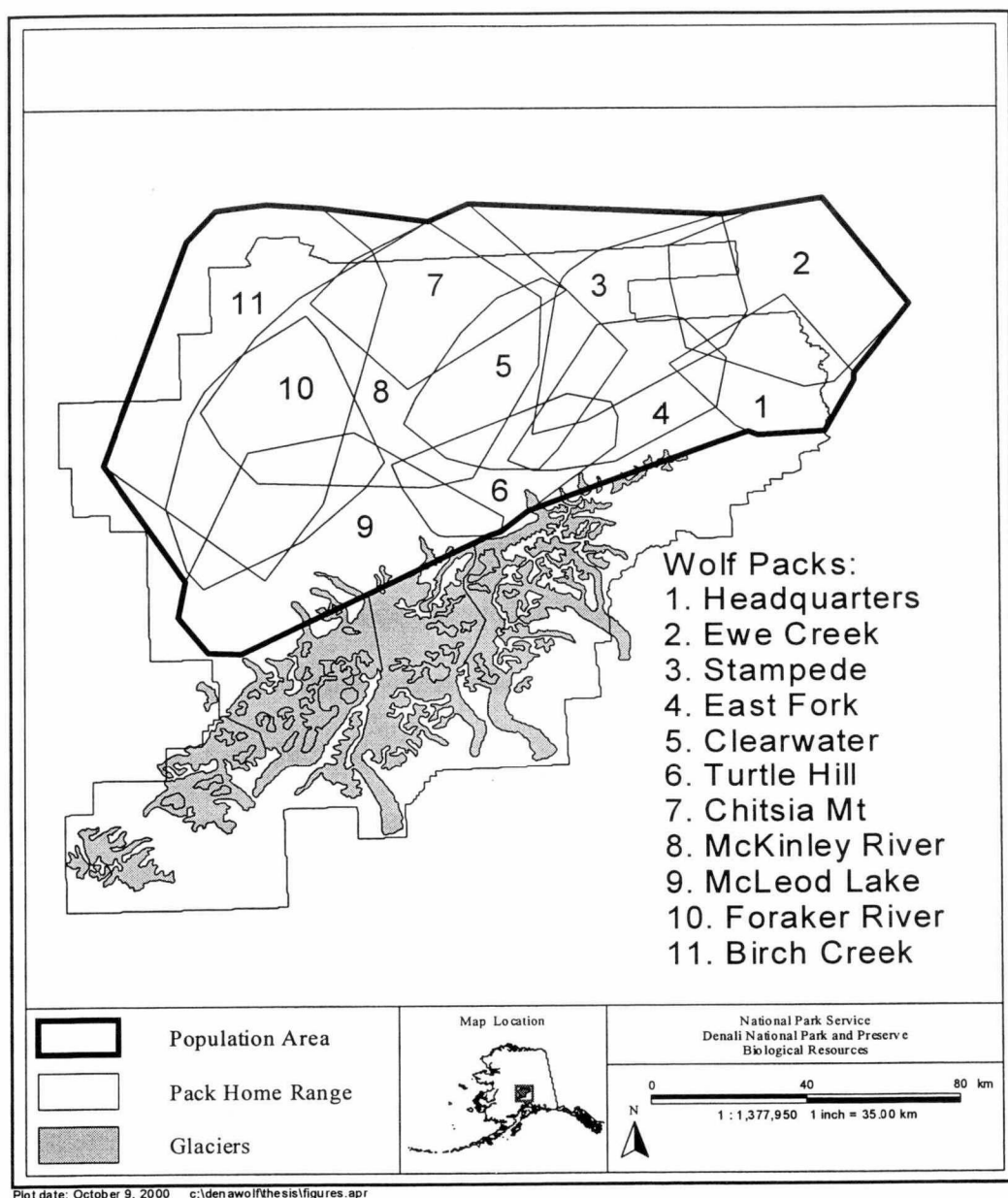


Figure 1. Location of Denali National Park and Preserve, Alaska. Population area (dark line) and individual pack home ranges (150 locations/pack) used for Monte Carlo simulations to evaluate monitoring strategies for wolves, based on field data from Denali National Park and Preserve, Alaska. 1986-1996.

The Alaska Range extends northeast to southwest through Denali and is characterized by mountain peaks >3,000 m, glaciers, and glacial valleys. In northeastern Denali the Alaska Range is flanked by lower mountains (<2,100 m) dissected by several major rivers flowing northward and two broad fault valleys perpendicular to the major drainages. Permanent snow and ice occur above 2,400 m, while lower mountains and foothills are covered predominantly by alpine sedge (*Carex spp.*) and shrub (*Salix spp.* and *Betula spp.*) tundras. Treeline occurs at about 800 m with spruce (*Picea spp.*) woodlands/forests, tussock (*Eriophorum spp.*) tundra, and riparian spruce/willow zones below. The western portion of Denali is characterized by the tundra foothills of the Mount McKinley/Foraker massif on the south extending northward into lowland flats with spruce forests, bogs and many north-flowing rivers.

Denali contains the only extensive area in Alaska or Canada where wolves and their prey have been largely protected from legal harvest for decades and on which a long history of information is available (Murie 1944, Haber 1977, Singer 1986, Mech et al. 1998).

Denali is a multi-predator/multi-prey ecosystem in which caribou (*Rangifer tarandus*), moose (*Alces alces*), and Dall sheep (*Ovis dalli*) comprise the main prey for wolves.

Denali is home to some 2,000 moose (Meier et al. 1991), 3,000-4,000 caribou, including those adjacent to the park that are within range of Denali wolf packs (Adams et al. 1989, Shults and Adams 1990), and approximately 2,400 Dall sheep (Singer 1984). In addition to wolves, a full complement of predators is present, including grizzly bear (*Ursus arctos*), black bear (*U. americanus*), a few coyotes (*Canis latrans*), lynx (*Lynx*

canadensis), red fox (*Vulpes vulpes*), wolverine (*Gulo gulo*) and other small mustelids and raptors.

Weather in the region is typical of a subarctic montane climate with temperatures ranging from 32 °C in summer to -47 °C in winter. Average annual precipitation at Denali headquarters on the eastern boundary is 38 cm, including 190 cm of snowfall. Murie (1944) and Mech et al. (1998) provide a more detailed description of the physiography, climate, wildlife, and vegetation of the area.

METHODS

Data presented here were collected during March 1986 through April 1996 as part of an ongoing radiotelemetry study of wolves at Denali. In general, the distribution and sizes of wolf packs were monitored by instrumenting wolves with radiocollars and locating them periodically from light aircraft (Mech 1980, Mech 1982, Mech et al. 1998).

Wolves were captured by darting from helicopters, primarily in November, March and April. Wolves were radiotracked 3 times per month on average, but summer tracking was less frequent. Radiolocations were mapped on 1:63,360 USGS topographic maps and subsequently converted to UTM coordinates. Any radiocollared companions were noted, and the total numbers of wolves observed were recorded. A 'location' that included more than 1 radiocollared wolf was treated as one observation (i.e. pack location) when collared wolves were less than 500 m apart.

I tried to maintain 2-3 collared wolves per pack, but the number varied from 1-11 depending on the success of capture attempts, survival of radioed wolves and other study objectives. For the purposes of this paper I eliminated 3 cases where > 4 wolves were collared in a pack to meet other study objectives. In those cases, locations from radiocollared wolves with the shortest tenures in the study were removed from the data set until 4 radiocollared wolves with the longest tenures remained. A few lone wolves were radiomarked throughout the study but were not included in any analyses. There were 3 instances where a pack of territorial wolves was reduced to a single individual. However, these individual wolves remained territorial within their same home range and were counted in the totals for each year. Therefore they were not considered as true non-territorial lone wolves.

Wolf Density Estimation

Wolf density was estimated twice a year, in late September – early October (Fall) when pups travel consistently with adults but can still be distinguished, and again in mid to late March (Spring) when packs approach their lowest numbers for the year and snow and adequate daylight provide good sightability from aircraft. For annual grouping of relocations, 1 May to 30 April was used as the biological year because pups are born in early May starting a new annual cycle (Mech et al. 1998).

The number of wolves, or numerator for density calculations, was the sum of individuals in instrumented packs within the study area (Table 1). Lone wolves were not included in any density estimates, except for the 3 cases where a pack of wolves was reduced to a single territorial individual. Although lone wolves can comprise up to 30% of a winter population (Fuller 1989), the sample of radiocollared wolves was biased to non-dispersing breeding wolves and pack members and did not provide reasonable estimates of lone wolves in the study area. Furthermore, the number of lone wolves may fluctuate widely within and among years depending on food availability (Mech et al. 1998). Therefore, my density estimates are for wolves within resident packs only and are conservative estimates of actual wolf abundance in the study area.

To determine the population area, or the denominator for the density estimates, I first determined the MCP for each pack territory. I used locations separated by ≥ 3 days to ensure independence of relocations as wolves usually take about 3 days to travel 40–50 km (a typical length of a wolf home range in interior Alaska) (Mech 1970, 1994; Mech et al. 1998). Extra-territorial forays and dispersals were not included by elimination of locations that were notably isolated (≥ 15 km) from other locations for a given pack. Fuller (1989) used ≥ 5 km for a definition of notably isolated locations in Minnesota where wolf home ranges are much smaller. Peterson et al. (1984) and Ballard et al. (1987, 1997) excluded forays and dispersals but did not provide a specific definition. Once pack territories were determined, the population area was calculated as the total area encompassed within the perimeter of the mosaic of pack territories. Areas within the

Table 1. Pack sizes of radiomarked wolf packs in spring (S; approximately 15 March) and fall (F; approximately 1 October), 1986 - 1996, Denali National Park and Preserve, Alaska.

| Pack | Year | | | | | | | | | | | | | | | | | |
|----------------|--------|-----|-----|-----|-----|-----|------|------|------|-----|------|-----|-----|-----|-----|-----|-----|-----|
| | S87 | F87 | S88 | F88 | S89 | F89 | S90 | F90 | S91 | F91 | S92 | F92 | S93 | F93 | S94 | F94 | S95 | F95 |
| Bearpaw | 5 | 10 | 4 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Beaver Fork | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 5 |
| Birch Creek | 7 | 11 | 11 | 23 | 23 | 15 | 16 | 16 | 15 | 11 | - | - | - | - | - | - | - | - |
| Castle Rocks | - | - | 2 | 8 | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Chilchukabena | - | - | - | - | - | - | - | 3 | 3 | 6 | 3 | 7 | - | - | - | - | - | - |
| Chitsia | - | - | - | 2 | 4 | 4 | 4 | 8 | 8 | 12 | 7 | 9 | 6 | 8 | 4 | 4 | - | - |
| Clearwater | 3 | 6 | 4 | 4 | 2 | 8 | - | - | - | - | - | - | - | - | - | - | - | - |
| Corner Lake | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 2 | 2 | 4 |
| East Fork | 6 | 8 | 7 | 19 | 18 | 27 | 24 | 33 | 18 | 16 | 11 | 15 | 10 | 9 | 6 | 9 | 9 | 14 |
| Ewe Creek | - | 8 | 5 | 5 | 4 | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Foraker | - | - | - | - | 2 | 7 | 7 | 9 | 4 | 8 | 3 | 7 | 6 | 6 | 7 | 6 | 9 | 12 |
| Headquarters | 1 | 2 | 2 | 7 | 7 | 14 | 10 | 11 | 9 | 10 | 7 | 5 | 4 | 9 | 2 | 6 | 2 | - |
| Highpower | - | - | 5 | 8 | 7 | 10 | 10 | 12 | 8 | 11 | 8 | 10 | - | - | - | - | - | - |
| Jenny Creek | - | - | - | - | - | - | - | - | - | - | - | - | - | 6 | - | - | - | - |
| Little Bear | - | - | - | 7 | 7 | 12 | 10 | 13 | 13 | 23 | 19 | 12 | 12 | 12 | 13 | 8 | 8 | - |
| McKinley River | - | 10 | 10 | 10 | 8 | 8 | 8 | 8 | 5 | 9 | 8 | 7 | 3 | 3 | 3 | 3 | 3 | 8 |
| McLeod Lake | 4 | 7 | 7 | 12 | 8 | 12 | 10 | 20 | 16 | 13 | 13 | 13 | 11 | 15 | 11 | 10 | 9 | 7 |
| McLeod West | - | - | - | - | - | - | - | - | - | 11 | 11 | 17 | - | - | - | - | - | - |
| Pirate Creek | - | - | 2 | 9 | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Sanctuary | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 2 | 2 | 5 |
| Savage | - | - | - | - | - | - | - | - | - | - | - | 5 | 3 | 8 | 6 | 9 | 5 | 9 |
| Slippery Creek | - | - | - | - | - | - | - | - | - | 5 | 3 | 1 | - | - | - | - | - | - |
| Stampede | - | - | - | 7 | 7 | 10 | 7 | 3 | 3 | 2 | 3 | 2 | 2 | 3 | 3 | 7 | 5 | 8 |
| Stony | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 2 | 2 |
| Swift Fork | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Thorofare | - | - | - | - | - | - | - | - | - | - | - | 2 | 2 | 7 | - | - | - | - |
| Turtle Hill | - | - | - | - | - | - | - | - | - | - | - | 8 | 7 | 7 | 6 | 6 | 3 | 6 |
| Windy | 6 | 8 | 6 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| TOTAL | Fall | - | 70 | - | 121 | - | 127 | - | 136 | - | 137 | - | 120 | - | 93 | - | 72 | - |
| | Spring | 32 | - | 65 | - | 98 | - | 106 | - | 102 | - | 96 | - | 66 | - | 61 | - | 59 |
| | MEAN | 4.6 | 7.8 | 5.4 | 9.3 | 7.5 | 11.5 | 10.6 | 12.4 | 9.3 | 10.5 | 8.0 | 8.0 | 6.0 | 7.8 | 6.1 | 6.0 | 4.9 |

territory mosaic too small to harbor an unmarked pack, but not included in any pack territory, were therefore included in the population area.

I evaluated the effects of radiolocation effort on estimates of home range size and investigated variation in home range size among years via multiple regression. Because I expected the relationship between home range size and radiolocation effort to be curvilinear, I compared regression results with radiolocation effort unmodified and transformed by square root and cube root (Devore and Peck 1986) and selected the model with the highest R^2 or best fit. To test for annual variation in home range size, I used stepwise regression to assess adding indicator variables for each year to the base regression equation with radiolocation effort. Therefore, I assumed that the relationship between home range size and radiolocation effort did not change among years.

Comparison of 2 Density Estimations

I calculated density estimates for Denali wolves utilizing radiolocation data grouped over 2 time periods to illustrate influences of sample size of radiolocations on population area and therefore estimates of wolf density. I used:

1 year of radiolocations: Density estimates within a biological year based on that year's radiolocations (e.g., Fall 1990 and Spring 1991 density estimates based on radiolocations during 1 May 1990-30 April 1991) (Fuller 1989, Mech et al. 1991).

2 years of radiolocations: Density estimates within a calendar year based on 2 biological years of radiolocations (e.g., Spring 1990 and Fall 1990 based on 1 May 1989-30 April 1991) (Mech et al. 1998).

I evaluated the influences of radiolocation effort on these density estimates by separately conducting multiple regression analyses on the 1-year and the 2-year estimates (18 estimates each; 2 per year for 9 years) with independent variables of mean pack size and mean number of radiolocations per pack. Mean pack size was included as the attribute of the population most likely to influence density, accounting for differences between spring and fall estimates, and was independent of sampling effort. I hypothesized that, because of their smaller samples of telemetry data, density estimates based on 1 year of telemetry data would be significantly correlated with radiolocation effort while the density estimates based on 2 years of telemetry data would not.

Evaluation of Effects of Radiolocation Effort and Number of Packs

To evaluate effects of radiolocation effort and the number of packs instrumented on estimates of population area, I conducted Monte Carlo simulations that approximated the methods described above for determining the population area and utilized a set of data derived from the field radiolocations. To conduct the simulations, the number of radiolocations had to be equal among packs and substantially larger than that normally used for estimating population area. I identified 11 regions of the study area that were

either inhabited continuously by one pack ($n = 5$) or consecutively by 2-3 packs ($n = 6$) (Fig. 1). For my simulation, I defined these 11 regions as "pack territories" and combined the 10 years of locations for packs that consecutively inhabited a given region. To standardize the sample size of radiolocations per pack, I systematically reduced each pack data set to 150 points (the maximum available for the pack with the fewest locations), by randomly deleting points that were ≤ 4 days apart, then ≤ 5 days apart, then ≤ 6 days apart, etc.

To conduct the Monte Carlo simulations, I modified a MCP home range program in SAS code (SAS Institute Inc. 1996, White and Garrott 1990: 343-349) to iteratively calculate population areas encompassed by any number of adjacent MCPs and allow some concavity between individual MCPs. Allowing for concavity in the population areas was also necessary because of the crescent shape of the Alaska Range along the southern boundary of the study area. Concavity was added to the population area polygon by evaluating each line segment of a large convex polygon incorporating all 11 packs. If a pair of adjacent corner points were from the same pack, the line segment they formed was included in the population area boundary. If not, the angle formed with every other location in the data set placed between the initial pair was determined and locations that formed angles $\geq 160^\circ$ were added as corners to the new concave polygon. The program sequentially evaluated each pair of corner points for the large, convex polygon, adding concavity where appropriate. The angle criteria of 160° was arrived at by trial and error. Once the concave population polygon was determined, the area of that polygon was calculated.

I automated the SAS program to iteratively resample the data set while I varied the number of radiolocations/pack randomly selected from the data set and the number of packs included in the analyses. I varied the number of radiolocations from 2 to 150 radiolocations per pack (2, 3, 4, 5, 10, 20, 30 . . . 150) and varied the number of packs from 1 to 11. For fewer than 11 packs, the program was constrained to select groups of packs that were contiguous. For every combination of sampling intensity and number of packs, I completed 100 iterations and recorded the population area size and the proportion of the maximum known area (with all 150 locations for the chosen packs) it represented.

Estimating Population Area via Nonlinear Regression

I evaluated the utility of applying NLR to provide an unbiased estimate and measure of precision of the true population area (the asymptote of the area-observation curve). I considered 4 curvilinear regression models of the appropriate form: 1) the Michaelis-Menton Equation (Brown and Rothery 1993: 345); 2) Holling's Disc Equation (Brown and Rothery 1993: 390); 3) Rational Function I (Parton and Innis 1972); and 4) the Natural Growth or Uptake Equation (Parton and Innis 1972). I selected Rational Function I:

$$Y = \frac{A}{1 + B/X} + \frac{C}{1 + D/X}$$

because of its flexibility to fit a variety of appropriate curve shapes and because the asymptote is specifically defined by the model parameters (asymptote = A+C).

With the data set used for the Monte Carlo simulations, I used iterative resampling to bootstrap estimates of the population area (the asymptote of the regression model) and associated variability (Efron 1979) while varying the sample size of radiolocations for all 11 packs. In each iteration for a given sample size of radiolocations, I randomized the order of points for each pack, and determined the population area sequentially with the addition of 1 point/pack until the predetermined sample size was reached. I then fit the regression function to the sequential area estimates, and recorded the asymptote estimate for that iteration. Occasionally, the regression analyses failed to converge on a solution or produced results that were unreasonably large ($>$ twice the area determined for 150 locations using conventional MCP methods) and those were not included in the analysis. The process was repeated until 100 successful iterations were accumulated for each level of radiolocation effort. I then ordered the asymptote estimates and determined the median, 90% confidence interval (90% CI; lower value = 6th ordered estimate, upper value = 95th ordered estimate) and percent confidence interval length (PCIL = 90% CI length/median). I use the median and PCIL instead of mean and variance because the estimates were not normally distributed but skewed by a few large estimates that greatly affected the means. To evaluate the success of NLR in correcting for sampling bias, I compared the median asymptotes for each level of radiolocation effort against the population area calculated from all 150 locations per pack using conventional MCP methods (Zar 1974: 145). I hypothesized that at some level of sampling effort within the range I evaluated, the estimate of population area would not differ from that determined

for the full data set (i.e., 150 locations/pack) and that PCIL would decrease with increasing radiolocation effort.

RESULTS

My data set included 3,746 independent locations (from 5,102 total) of 138 radiocollared wolves from 28 packs during March 1986-April 1996 (Table 2). Overall, radiolocation effort averaged 32 independent locations per pack each year, but annual radiolocation effort varied from 3 to 152 locations for individual packs (Fig. 2). Small sample sizes (<10 radiolocations) resulted from packs instrumented late in the biological year ($n = 12$), packs that did not persist through the year ($n = 4$), loss of radio contact with packs ($n = 2$), and packs that were far from my base of operation during a year of limited funding ($n = 3$). The 2 packs with >100 radiolocations occurred during the first year of the project when few packs were radiomarked, funding was abundant, and each pack had 3 collared individuals that were frequently apart.

Average radiolocation effort per year ranged from 21 to 52 radiolocations/pack (Table 2). Home range sizes based on 1 year of radiolocations averaged 864 km^2 (Table 3) (including 21 home range estimates derived from <10 radiolocations) and were curvilinearly correlated with radiolocation effort (Fig. 3A, $r^2 = 0.780$, $P < 0.001$). With variability in radiolocation effort accounted for, average home range sizes were not significantly different among years ($P \geq 0.075$).

Table 2. Independent* radiolocations obtained for each wolf pack each biological year (e.g., 87 = 1 May 1987 – 30 April 1988), 1986 - 1996, Denali National Park and Preserve, Alaska.

| Pack | Year | | | | | | | | | |
|----------------|------|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| | 86 | 87 | 88 | 89 | 90 | 91 | 92 | 93 | 94 | 95 |
| Bearpaw | 3 | 55 | - | - | - | - | - | - | - | - |
| Beaver Fork | - | - | - | - | - | - | - | - | - | 13 |
| Birch Creek | 4 | 49 | 42 | 26 | 30 | 22 | - | - | - | - |
| Castle Rocks | - | 7 | 34 | - | - | - | - | - | - | - |
| Chilchukabena | - | - | - | - | 12 | 22 | 9 | - | - | - |
| Chitsia | - | - | 9 | 27 | 22 | 32 | 18 | 9 | 4 | - |
| Clearwater | 152 | 73 | 75 | 39 | - | - | - | - | - | - |
| Corner Lake | - | - | - | - | - | - | - | - | 6 | 41 |
| East Fork | 110 | 71 | 68 | 47 | 65 | 47 | 37 | 25 | 37 | 55 |
| Ewe Creek | - | 29 | 42 | - | - | - | - | - | - | - |
| Foraker | - | - | 18 | 19 | 25 | 25 | 15 | 8 | 31 | 57 |
| Headquarters | 66 | 45 | 63 | 49 | 49 | 36 | 26 | 19 | 31 | - |
| Highpower | - | 5 | 21 | 13 | 12 | 9 | 3 | - | - | - |
| Jenny Creek | - | - | - | - | - | - | - | 8 | 8 | - |
| Little Bear | - | - | 5 | 30 | 14 | 45 | 15 | 15 | 34 | 10 |
| McKinley River | - | 9 | 34 | 5 | 24 | 36 | 31 | 15 | 30 | 45 |
| McLeod Lake | 13 | 56 | 64 | 48 | 44 | 32 | 56 | 41 | 32 | 34 |
| McLeod West | - | - | - | - | - | 22 | 7 | - | - | - |
| Pirate Creek | - | 7 | 19 | - | - | - | - | - | - | - |
| Sanctuary | - | - | - | - | - | - | - | - | 4 | 43 |
| Savage | - | - | - | - | - | - | 14 | 22 | 39 | 36 |
| Slippery Creek | - | - | - | - | - | 18 | 14 | - | - | - |
| Stampede | - | - | 31 | 30 | 12 | 31 | 25 | 16 | 36 | 44 |
| Stony | - | - | - | - | - | - | - | - | 5 | 35 |
| Swift Fork | - | - | 17 | - | - | - | - | - | - | - |
| Thorofare | - | - | - | - | - | - | 21 | 15 | - | - |
| Turtle Hill | - | - | - | - | - | - | 28 | 57 | 42 | 37 |
| Windy Creek | 14 | 51 | - | - | - | - | - | - | - | - |
| TOTAL | 362 | 457 | 550 | 333 | 309 | 377 | 319 | 250 | 339 | 450 |
| MEAN | 52 | 38 | 37 | 30 | 28 | 29 | 21 | 21 | 24 | 38 |

* Independent locations are ≥ 3 days apart.

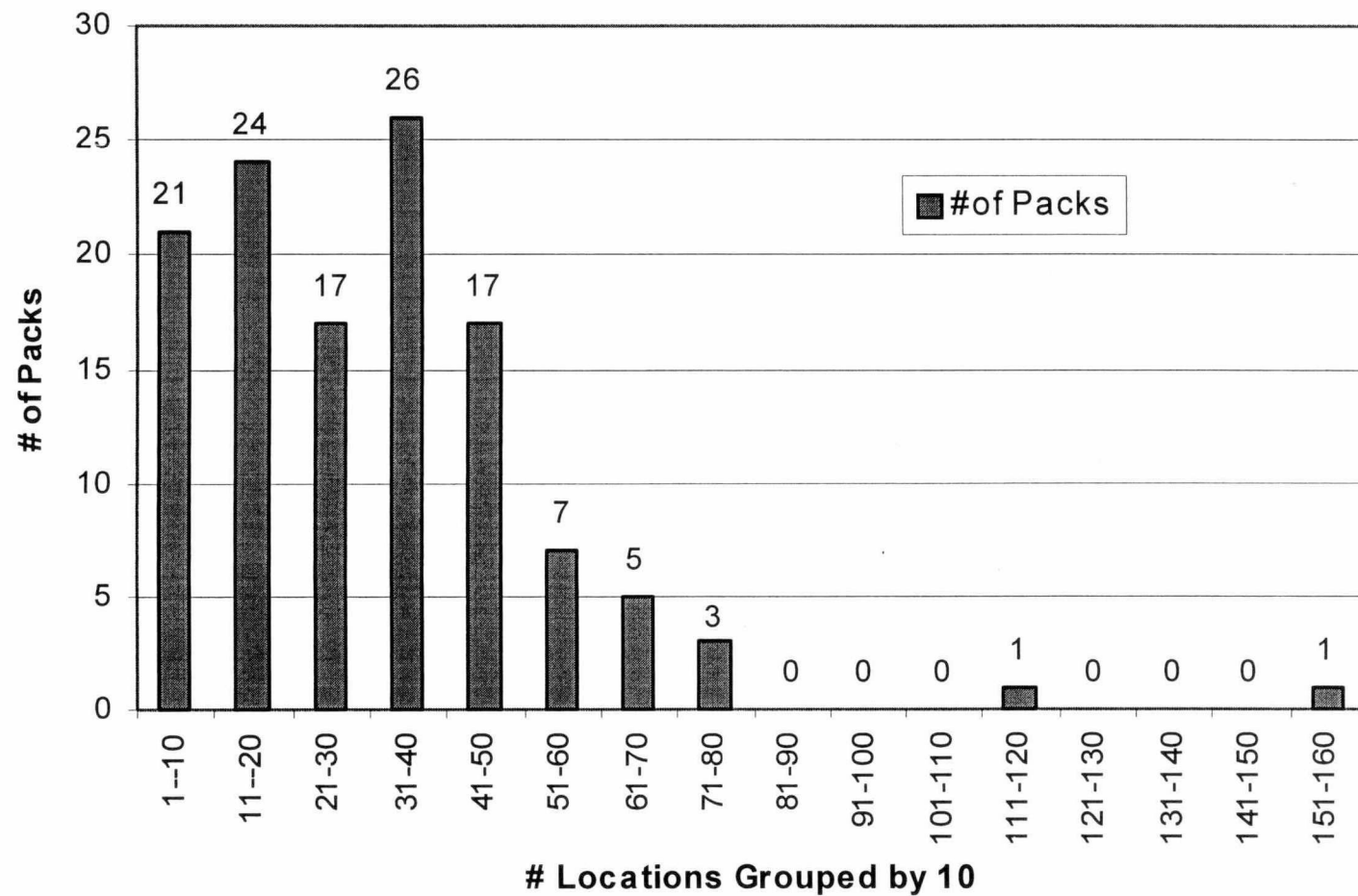


Figure 2. Distribution of sample size of locations per pack per year for wolf packs in Denali National Park and Preserve, Alaska, 1986 – 1996.

Table 3. Comparison of wolf densities (wolves/1,000km²), mean locations per pack, and mean home range size calculated using 1 year of radiolocations vs. 2 years of radiolocations to determine population area, with mean pack size and number of packs used in the calculations, 1986 - 1996, Denali National Park and Preserve, Alaska.

| | <u>Wolf Density</u> | | <u>Ratio</u> 1yr/2yr | <u>Mean PackSize</u> | | <u>Number of Packs</u> | | <u>Mean</u> <u>Locations/Pack</u> | | <u>Mean Home</u> <u>Range Size (km²)</u> | |
|---------------|---------------------|--------|-------------------------|----------------------|--------|------------------------|--------|--------------------------------------|--------|--|--------|
| | 1 Year | 2 Year | | 1 Year | 2 Year | 1 Year | 2 Year | 1 Year | 2 Year | 1 Year | 2 Year |
| Fall | | | | | | | | | | | |
| 87 | 8.0 | 5.7 | 1.40 | 7.8 | 7.8 | 8 | 8 | 49 | 89 | 1092 | 1448 |
| 88 | 9.4 | 9.0 | 1.04 | 9.3 | 9.9 | 12 | 11 | 42 | 71 | 1113 | 1345 |
| 89 | 11.0 | 8.8 | 1.25 | 11.5 | 11.5 | 10 | 11 | 30 | 70 | 905 | 1687 |
| 90 | 11.1 | 10.7 | 1.04 | 12.4 | 12.4 | 11 | 11 | 28 | 55 | 847 | 1216 |
| 91 | 11.5 | 9.5 | 1.21 | 10.5 | 10.5 | 12 | 13 | 31 | 53 | 816 | 1141 |
| 92 | 9.4 | 9.6 | 0.98 | 7.2 | 8.0 | 12 | 15 | 25 | 45 | 642 | 940 |
| 93 | 14.0 | 8.9 | 1.57 | 8.1 | 7.9 | 9 | 11 | 25 | 48 | 497 | 829 |
| 94 | 7.8 | 7.0 | 1.11 | 6.8 | 6.4 | 9 | 10 | 32 | 50 | 850 | 948 |
| 95 | 7.6 | 7.2 | 1.06 | 7.3 | 7.3 | 11 | 12 | 40 | 64 | 949 | 1310 |
| Mean | 10.0 | 8.5 | 1.18 | 9.0 | 9.1 | 10.4 | 11.3 | 34 | 61 | 857 | 1207 |
| Spring | | | | | | | | | | | |
| 87 | 3.8 | 3.0 | 1.27 | 4.0 | 4.6 | 5 | 7 | 71 | 109 | 1026 | 1687 |
| 88 | 6.6 | 4.6 | 1.43 | 5.8 | 5.4 | 8 | 12 | 45 | 79 | 1019 | 1442 |
| 89 | 7.1 | 6.1 | 1.16 | 7.5 | 7.5 | 12 | 13 | 41 | 65 | 1129 | 1540 |
| 90 | 9.5 | 8.3 | 1.14 | 10.6 | 10.6 | 9 | 10 | 29 | 59 | 953 | 1298 |
| 91 | 8.4 | 7.5 | 1.12 | 9.3 | 9.3 | 11 | 11 | 28 | 59 | 847 | 1233 |
| 92 | 8.5 | 7.9 | 1.08 | 8.0 | 8.0 | 11 | 12 | 32 | 51 | 855 | 1064 |
| 93 | 7.2 | 6.8 | 1.06 | 6.0 | 6.0 | 11 | 11 | 26 | 48 | 656 | 829 |
| 94 | 10.1 | 6.1 | 1.66 | 6.3 | 6.1 | 8 | 10 | 26 | 54 | 503 | 1038 |
| 95 | 6.3 | 4.9 | 1.29 | 5.5 | 4.9 | 9 | 11 | 32 | 64 | 852 | 1274 |
| Mean | 7.5 | 6.1 | 1.22 | 7.0 | 6.9 | 9.3 | 10.8 | 37 | 65 | 871 | 1267 |

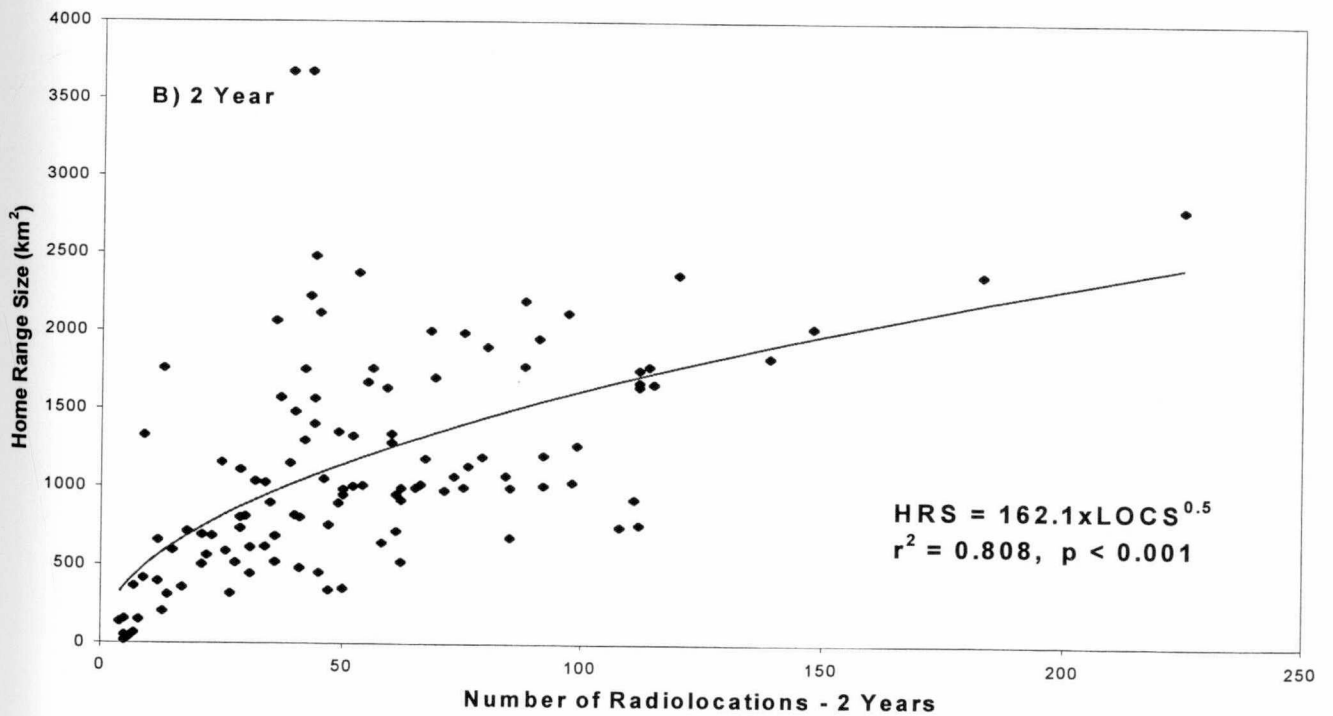
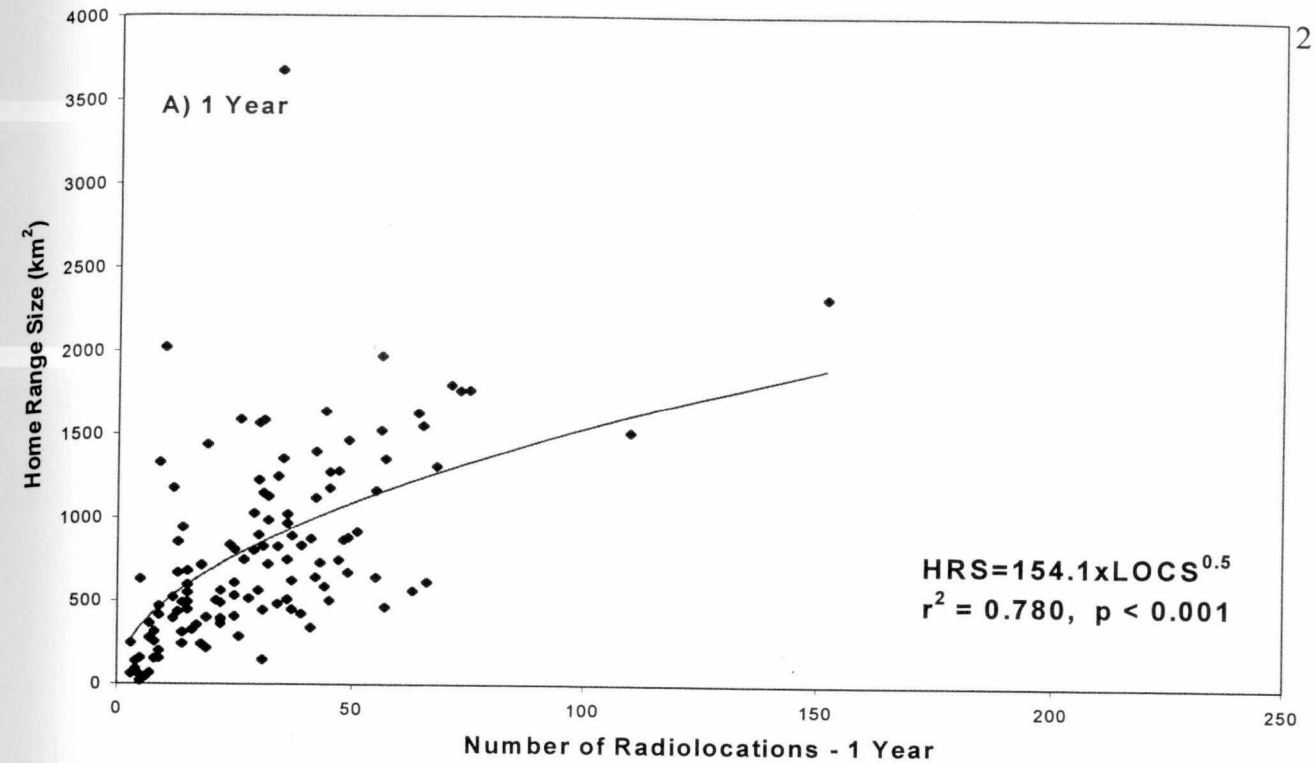


Figure 3. Relationships between wolf home range size (HRS) and radiolocations/pack (LOCS) for A) data accumulated over 1 year, and B) data accumulated over 2 years during 1986 – 1996, Denali National Park and Preserve, Alaska.

When radiolocation data were combined over 2 years, I averaged 63 radiolocations/pack overall and annual averages ranged from 45–109 radiolocations/pack (Table 3). Home range sizes based on 2 years of radiolocation data averaged 1,237 km², or 43% larger than the 1-year home ranges, and again were curvilinearly correlated with radiolocation effort (Fig. 3B, $r^2 = 0.808$, $P < 0.001$). With radiolocation effort accounted for, 2-year home range sizes were significantly larger in 1989 than in other years ($P = 0.025$). However, if one unusually large territory (McKinley River) was deleted, the 1989 year effect was no longer significant ($P = 0.259$).

Pack sizes averaged 6.9 wolves (range = 4.6–10.6) and 9.0 wolves (range = 6.0–12.4) in spring and fall, respectively (Table 1). Pack sizes were lowest in spring 1987 (mean = 4.6) and highest during fall 1990 (mean = 12.4). On average, mean pack size declined by 24% from October to March by natural attrition, including dispersal and natural mortality. Human harvest had very little effect (Mech et al. 1998).

Density Estimation

Density estimates based on 1 year of radiotelemetry data (mean = 35 locations/pack) were higher than those based on 2 years of telemetry data (mean = 63 locations/pack) for all estimates except fall 1992, and averaged 22% (1.4 wolves/1000 km²) higher (Table 3, Fig. 4). However, differences between the 1 and 2 year estimates for the same season varied widely, ranging up to 66%, or 4.0 wolves/1,000 km², for spring 1994. Density estimates within 1 biological year, Fall 93 and Spring 94, showed the greatest spread

between densities calculated via the 2 methods (Fig. 4). One-year densities during that winter were based on the lowest mean number of radiolocations/pack (25 and 26, respectively) and involved few packs (9 and 8, respectively). These 1-year densities were the highest calculated for the study, though mean pack size was below average (8.1 and 6.3, respectively).

Density estimates derived from 1 year or 2 years of telemetry data were significantly correlated with radiolocation effort (MLOC) ($P = 0.016$ and < 0.001 , respectively), as determined via multiple regression with mean pack size included in the regression models (Table 4). However, the multiple regression accounted for 91% of the variability in the 2-year estimates, but only 65% for the 1-year estimates. Further, the regression coefficient for radiolocation effort in the 1-year analysis was 63% greater than that for the 2-year analysis (Table 4), indicative of the greater influence of radiolocation effort on the 1-year density estimates.

Using the resulting regression equations, I adjusted each density estimate for differences in radiolocation effort by using the grand mean number of radiolocations (35 and 63 for the 1 and 2-year analyses, respectively) in place of the annual means (Fig. 5). This essentially standardized the radiolocation effort to the mean level over the entire study. The resulting density estimates were scaled directly to mean pack size because it was the only other variable in the regression equations. These adjustments had a greater influence on the 1-year estimates than the 2-year estimates, as expected from the R^2

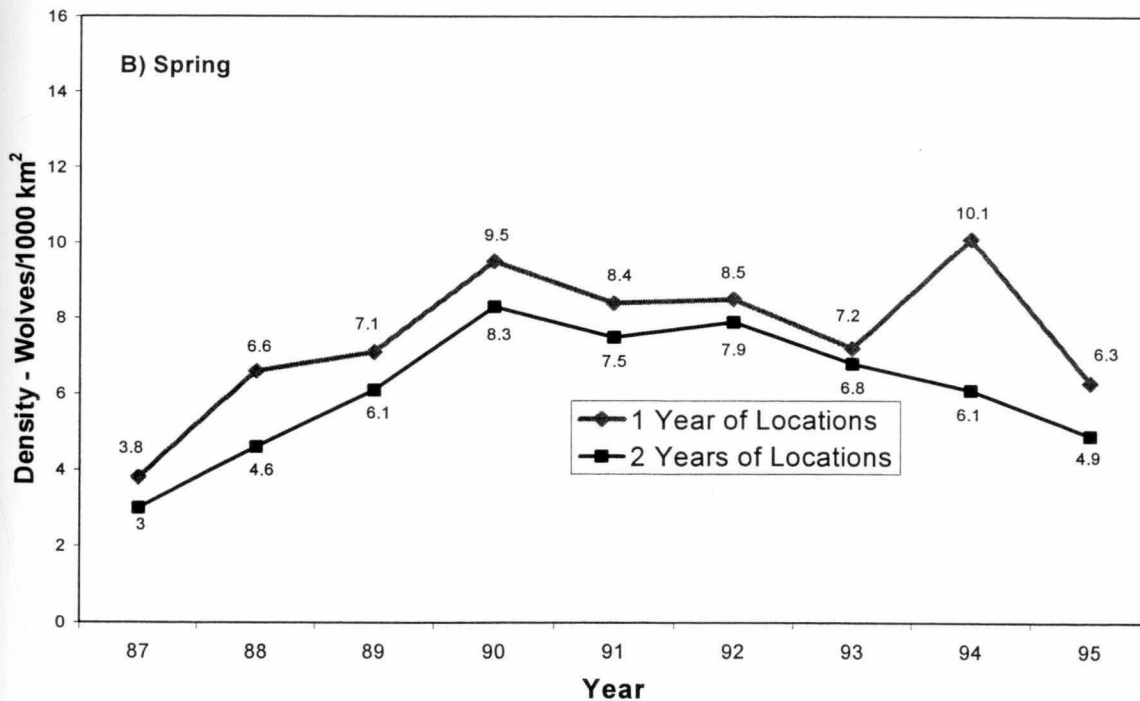
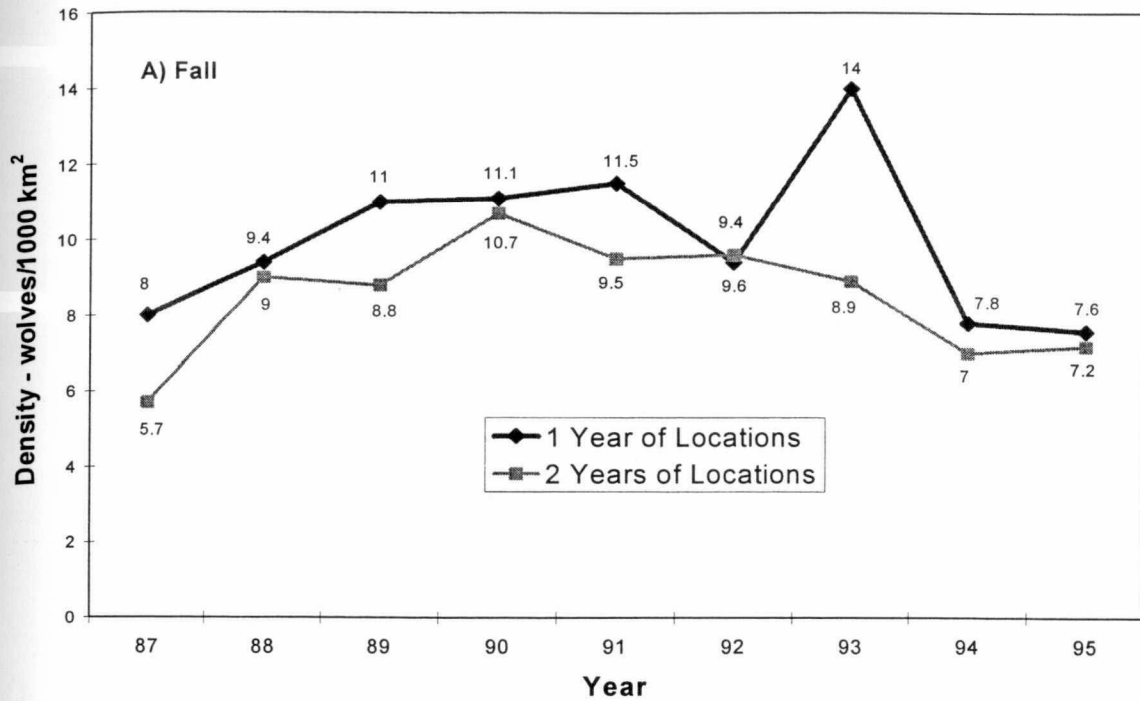


Figure 4. Fall (A) and spring (B) wolf densities (wolves/1000km²) by year for 2 sampling intensities. Denali National Park and Preserve, Alaska, 1986 – 1996.

Table 4. Results of multiple regression to determine relationships between wolf density (wolves/1,000 km²), mean pack size (MPS), and radiolocation effort, or mean locations per pack (MLOC), for density estimates based on 1 or 2 years of radiolocation data from Denali National Park and Preserve, Alaska, during 1986 – 1996.

| Variable | Coefficient | <i>t</i> | <i>P</i> |
|--|-------------|----------|----------|
| Population area based on 1 year of radiolocation data; MLOC = 25 – 71. | | | |
| CONSTANT | 7.879 | 3.54 | 0.003 |
| MPS | 0.512 | 2.94 | 0.010 |
| MLOC | -0.093 | 2.71 | 0.016 |
| n = 18 cases, R ² = 0.650 | | | |
| Population area based on 2 years of radiolocation data; MLOC = 45 – 109. | | | |
| CONSTANT | 5.879 | 6.09 | <0.001 |
| MPS | 0.625 | 8.79 | <0.001 |
| MLOC | -0.057 | 5.73 | <0.001 |
| n = 18 cases, R ² = 0.909 | | | |

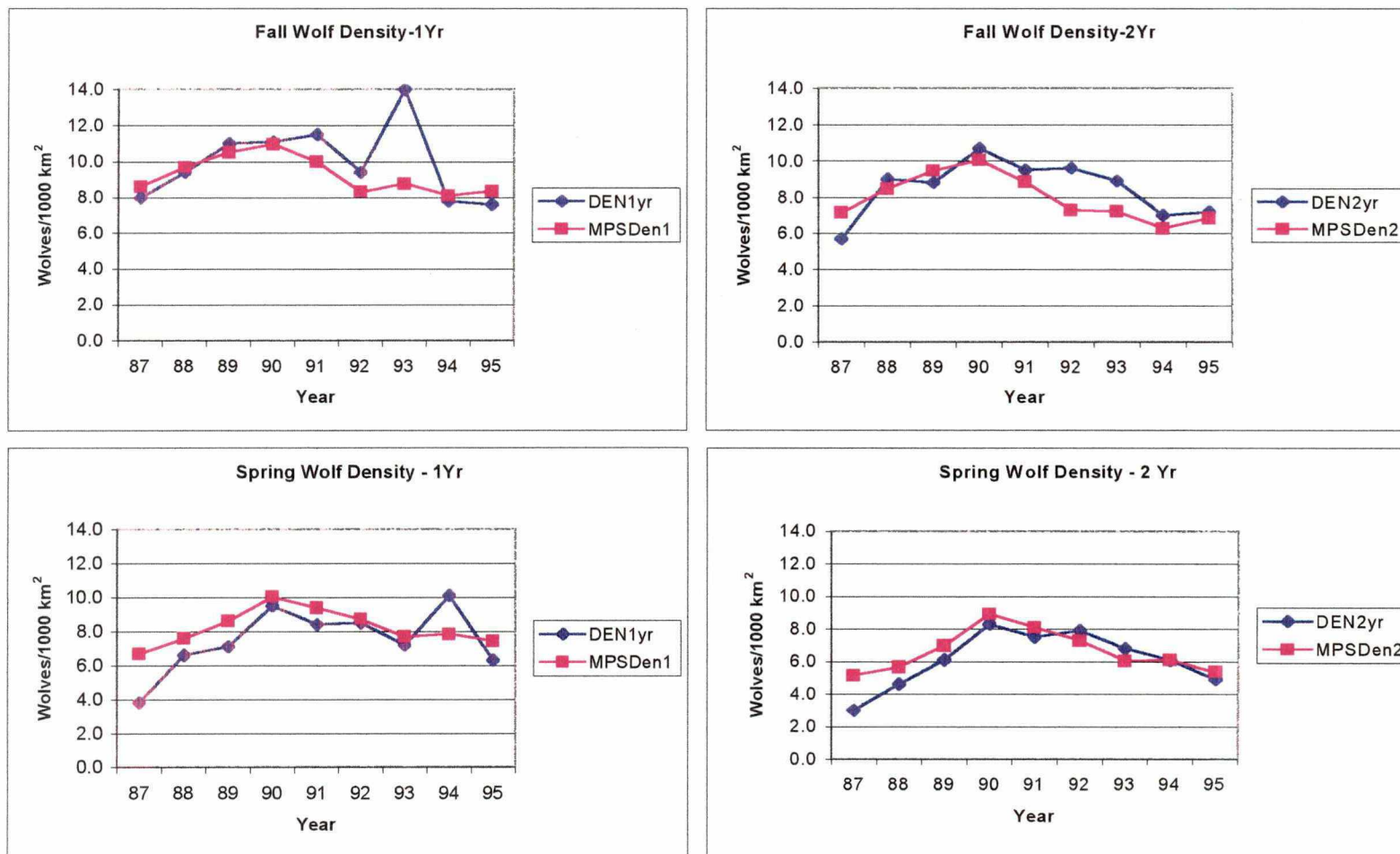


Figure 5. A comparison of fall and spring wolf densities for 1 year and 2 years of radiolocations. Each graph contrasts densities calculated in the standard way (DEN) to those standardized for radiolocation effort at the mean level over the entire study (MPSDen). Denali National Park and Preserve, Alaska, 1987 – 1995.

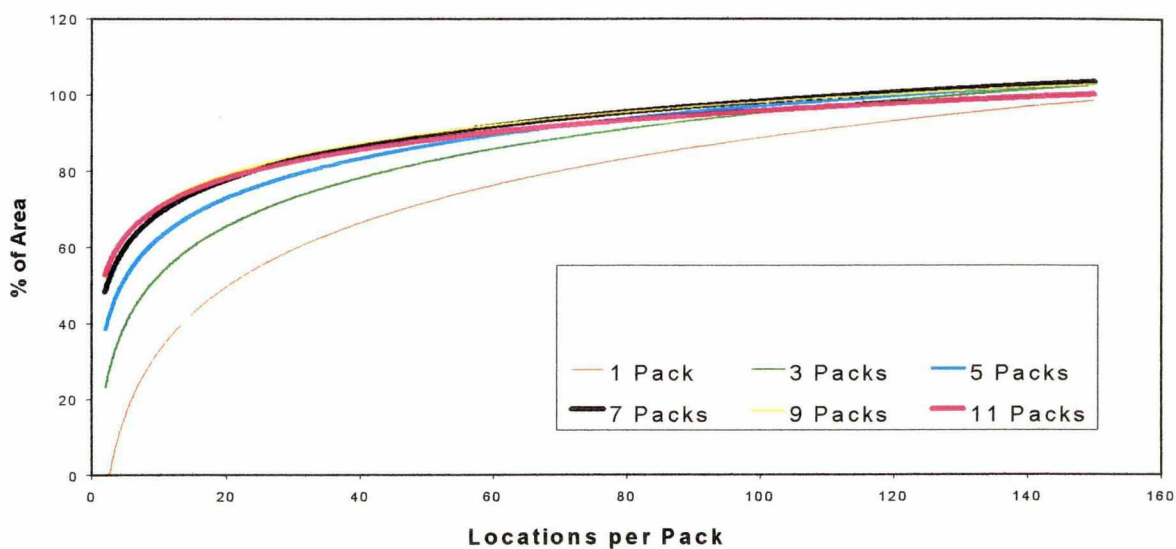
values for the regressions. For the density estimates based on 2-years of radiolocations, the most noticeable effect was to inflate the density estimate for Spring 1987, when radiolocation effort was the greatest (Table 3, Fig. 5).

Effects of radiolocation effort and number of packs

A substantially greater proportion of the population area was determined at low sample sizes for 11 packs together than for a home range of a single pack (Fig. 6A). For example, with only 5 locations/pack, the estimate of population area was 63% of the total area (based on 150 locations/pack) for 11 packs, compared to only 10% for a single pack territory. Variability in estimates of population area were substantially lower for groups of packs than individual pack territories as well (Fig. 6B). For 11 packs, 60 locations encompassed 90% of the total area and the area increased $< 1\%$ with each additional 5 locations.

Location-area curves for intermediate numbers of packs fell between the relationships for a single pack and the entire population of 11 packs (Fig. 6A). As the number of packs increased, the proportion of the total area estimated for a given radiolocation effort increased but differed little for > 6 packs. Therefore, achieving a threshold of the proportion of the population area determined (Fig. 6A) or of the benefit of additional radiolocations as (Fig. 7) required fewer radiolocations as the number of packs increases.

A) Percent Area



B) Coefficient of Variation

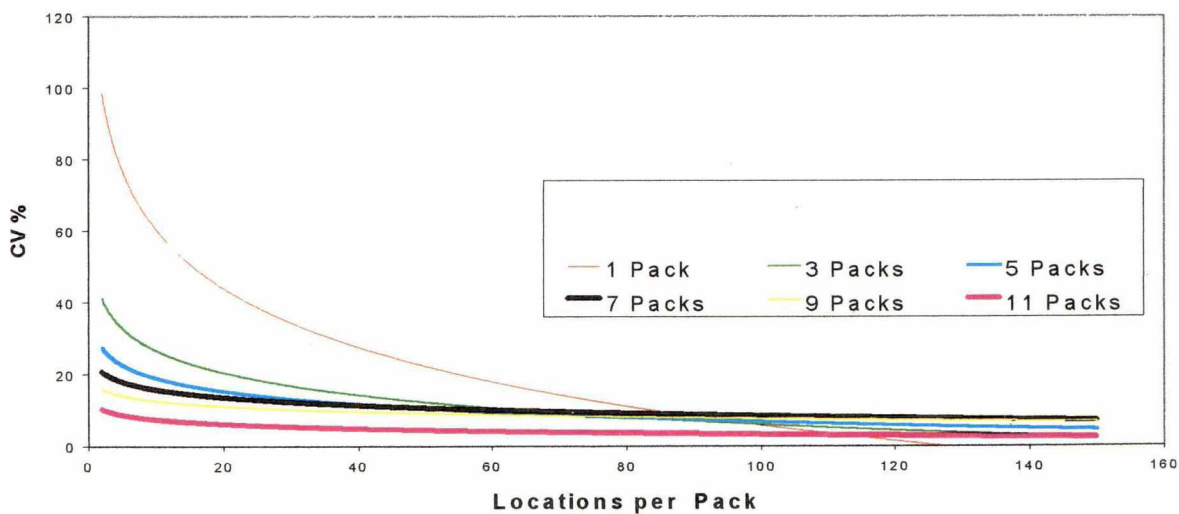


Figure 6. Percent of wolf population area measured and coefficient of variation for sampling intensities ≤ 150 locations per pack and ≤ 11 adjacent wolf packs. Results are from Monte Carlo simulations to evaluate monitoring strategies for wolves based on field data from Denali National Park and Preserve, Alaska, 1986 – 1996. Only six of 11 lines are shown for clarity.

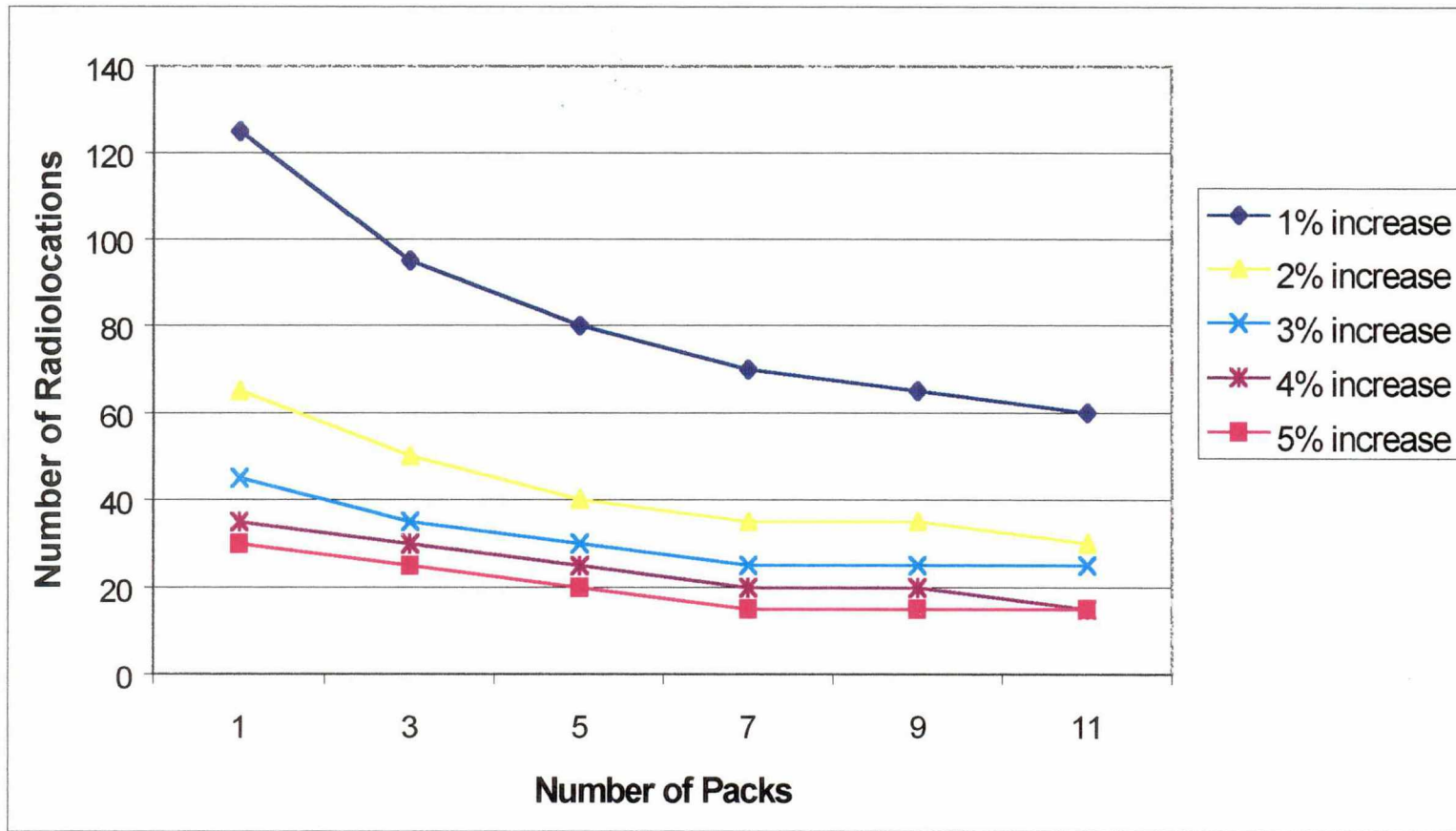
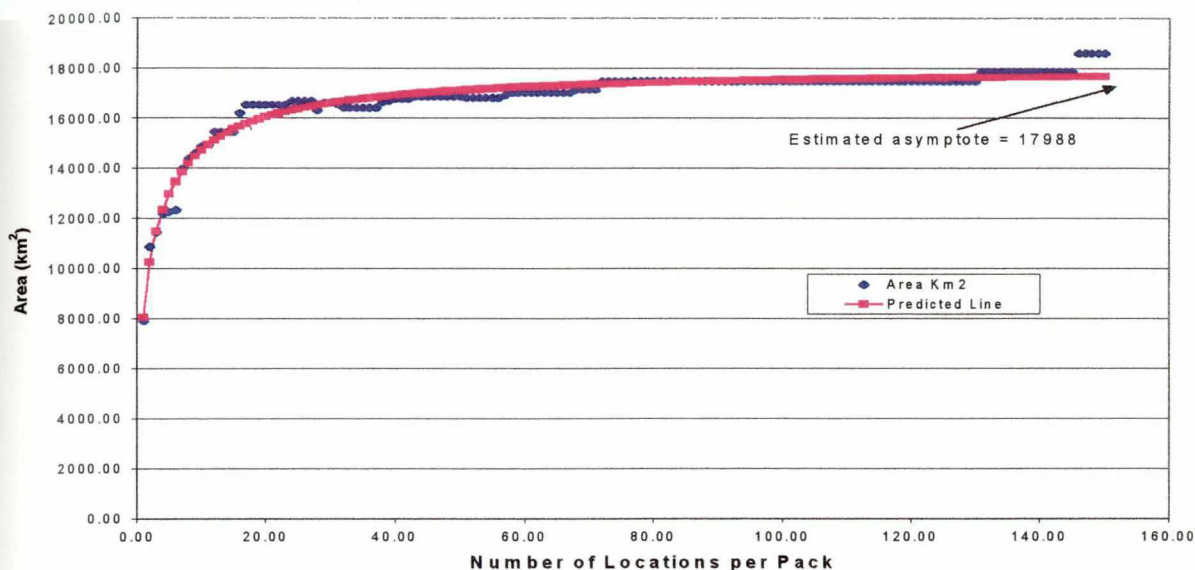


Figure 7. Thresholds of radiolocation effort at which an additional 5 locations per wolf pack would result in the specified (1-5%) increase in population area, based on Monte Carlo simulations of wolf telemetry data. Denali National Park and Preserve, Alaska, 1986 – 1996.

A) Line plateaus quickly



B) Line continues to increase rapidly

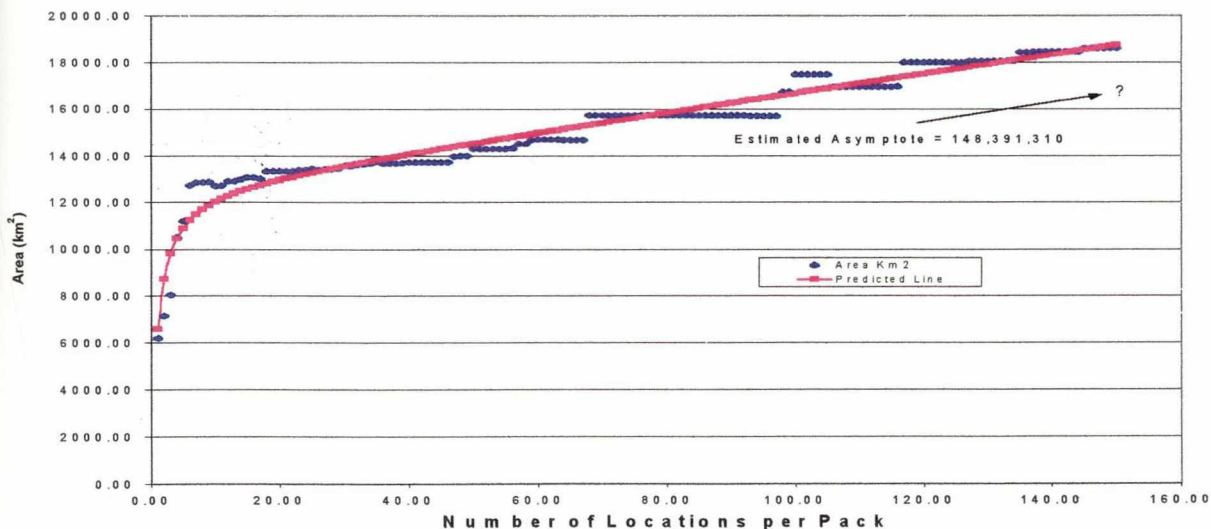


Figure 8. Examples of fitted lines of predicted values showing (A) a line quickly attaining an asymptote and predicting one of the lower estimates. (B) a rapidly increasing line not close to an asymptote predicting a very high estimate. Each line is simply a different random order of all the data, each one predicting a different asymptote for the population area for wolves in Denali National Park and Preserve Alaska, 1986 - 1996.

Prediction of population area using nonlinear regression

In general, use of NLR to account for sampling bias was unsuccessful. Over the range of radiolocation effort I evaluated (10-150 locations/pack), NLR, or bias corrected, population areas were all less than the estimate for the entire data set of 150 locations per pack (Table 5). Further, the percent bias did not decrease with increasing radiolocation effort as expected (linear regression, $t = 0.20$, 1 df, $P = 0.846$), averaging 11% throughout. Precision of the extrapolation did improve with increasing radiolocation effort (linear regression of PCIL, $t = 2.67$, 1 df, $P = 0.032$) but was generally poor (Table 5). The poor precision is illustrated by the random ordering of the same 150 locations per pack resulting in some curves that plateaued quickly while others continued to increase (Fig. 8 A & B).

DISCUSSION

Although there has been substantial analysis and discussion of the effects of radiolocation effort on home range estimation for wolves (Fritts and Mech 1981, Bekoff and Mech 1984, Peterson et al. 1984, Fuller 1989, Ballard et al. 1998), no one has broached the subject for density estimation. Fuller and Snow (1988) provided recommendations for estimating density (30–35 radiolocations per pack) but their recommendations were based on the potential for missing wolf packs within the population area and the diminishing returns of additional radiolocations, not on effects of sampling on density estimation.

Density estimates based on the number of locations I acquired in an average year, and comparable to the recommendations of Fuller and Snow (1988), were significantly influenced by radiolocation effort. From my regression analysis of density estimates based on 1 year of telemetry data, 5 additional radiolocations would decrease density estimates by about 5%. My Monte Carlo simulation results show that increasing the radiolocation effort from 30 to 40 locations per pack produced a 3% increase in population area for 11 packs and a 5% increase for 5 packs. Densities based on about twice the radiolocations were still influenced by radiolocation effort, but the influence was reduced. The effects of sampling I noted may be lessened in the Denali study because much of the southern boundary of the population area is determined by high mountain habitats unsuitable for wolves or their prey, forming a relatively fixed southern boundary for my population areas. Sampling effects could be greater in areas of continuous wolf habitat.

Density estimation also can be influenced by the number of packs monitored. From my analysis, 6 packs appears to be the threshold where additional monitoring effort is no longer necessary to compensate for small numbers of adjacent packs. Monitoring designs for future wolf studies should take this into account.

Although my results point to maximizing the number of packs and the number of radiolocations/pack, I did not address the issue of overlap with surrounding packs that were not included in the density estimate. Based on the above analyses, as radiolocation

effort increased, population area also increased and estimated density declined.

However, if overlap with other adjacent wolf packs not included in the count of wolves for the density estimate, also increased, then this source of error would counteract the radiolocation effort error to some unknown degree.

Lone wolves are another source of error in estimating wolf density. In this analysis, lone non-territorial wolves were ignored. Because the density estimates in this study represent wolves in resident packs only, the estimates must be considered conservative. Estimating the number of lone wolves in a population at any given time is difficult as the number probably fluctuates widely depending on prey abundance and vulnerability, as well as overall wolf density (Mech et al. 1998). Using the proportion of collared wolves that are lone wolves is a tempting solution, however, dominant individuals are often targeted when immobilizing wolves from helicopters. The sample of collared wolves is therefore not representative of the population, with lone wolves poorly represented. When wolves are trapped it may be more reasonable to use the proportion of collared lone wolves as an indicator of the number in the population (Fuller 1989) because trapping is less selective.

Effects of inadequate radiolocation effort on density estimates may be more pronounced in low density wolf populations found in Alaska (average of 8 wolves/1,000 km² for this study) as compared to the much higher densities found in Minnesota (40 wolves/1,000 km², Fuller 1989) or Isle Royale Michigan (90 wolves/1,000 km², Peterson and Page 1988). The much larger home ranges found in Alaska result from lower densities of prey.

Fuller (1989) discussed the strong correlation between wolf densities and ungulate biomass. When prey densities are low, wolves must travel over larger areas producing territories that are difficult if not impossible for wolves to travel across in a day. In contrast, wolves in Minnesota can easily travel across their territory in a day (Mech 1970, 1994). Furthermore, territories in Alaska or Canada may include areas used only seasonally in response to migratory prey. These factors also play a role in determining independence of locations.

The application of NLR to account for biases in wolf density estimates related to radiolocation effort was generally unsuccessful. Estimates of population area derived from NLR at lower sampling intensities were significantly less than the NLR estimate at 150 locations per pack and estimated bias did not change overall levels of radiolocation effort examined (10-120 locations/pack). To adequately define an asymptotic curve, data must cover a wide range of the independent variable so the rate of increase or slope of the curve, has declined substantially, resulting in reduced variability in estimates of the asymptote. The range of radiolocation effort that is of interest, however, is in the lower end of the range where the underlying function is still rising and the asymptotic value cannot be predicted with precision.

There were at least 2 sources of variation in my NLR simulations. Variation resulted from selecting a different set of points for each iteration, which is more important at low sampling intensities, declining with higher radiolocation effort. The second source of

variation was derived from reordering of the points in each iteration. At 150 locations per pack (using all the data) the variability due to the ordering of the points is the only source left, however this variability was still very large and had a large effect on the outcome of the analysis. Even with the same 150 data points random ordering of points resulted in curves that plateaued quickly, while others continued to increase (Fig. 8 A & B), and in some cases the NLR could not converge on a solution or gave implausible results.

This analysis points to the need for caution in making assumptions about the precision of wolf density estimates. Variation in radiolocation effort makes comparisons among years or among studies problematic. Density estimates from a variety of studies have been compared to one another with no evaluation of variability in radiolocation effort (e.g., Fuller 1989) with the assumption that the reported estimates are directly comparable.

One alternative that alleviates the problems with using density estimates to compare trends within wolf populations is to use mean pack size. Mean pack size is the variable with the greatest influence on wolf density that is not affected by radiolocation effort. Therefore, it should provide an index of population trends within a individual population. However, mean pack size cannot be used to compare different wolf populations because similar mean pack sizes may correspond to widely different densities throughout the geographic range of wolves. For example, densities may differ nearly 10 fold between

interior Alaska and northern Minnesota (Mech 1973, Peterson and Page 1988, Fuller 1989, Mech et al. 1998) but mean pack sizes can be similar.

There are several practical limitations to gathering data to estimate a wolf density. First, it is very expensive to capture and collar wolves initially and even more expensive to adequately relocate them. Weather and pilot/aircraft availability also limit radiolocation efforts. These factors add up and make it difficult to acquire > 40 independent locations annually. In fulfilling other study objectives wolves may be found once or twice a day during certain times of the year and many locations can accumulate in a short period of time. However, only a small proportion of these locations would be considered independent as defined by this study (3 or more days apart).

With the advent of satellite collars (Ballard et al. 1995, 1998) and Global Positioning System (GPS) collars (Moen et al. 1996, Rodgers et al. 1996) that can store locations frequently (for example, a location every hour, 24 hours a day), a researcher is no longer sampling, and each location is dependent on the previous one, rendering independence of locations as a non-issue. This new technology comes at a price however, with satellite and GPS collars costing ≥ 10 times that of a conventional collar. Also, most GPS collars of acceptable size store location data onboard and the collar must be retrieved. Therefore if the animal disperses or the collar fails, all data are lost. Battery life for most wolf-sized GPS collars rarely exceeds 1 year (compared to 3 or 4 years for conventional collars) so study animals need to be captured more frequently. Wolves with GPS or satellite collars

still need to be found from aircraft to determine pack size, although not as often. Finally, there is usually high turnover of wolves from dispersals and mortality necessitating the need to maintain 2 or 3 radiocollared wolves in each pack. When these factors are combined, using GPS collars routinely as a replacement to conventional collars is currently prohibitively expensive.

MANAGEMENT IMPLICATIONS

Radiotelemetry is probably the most common method used to monitor wolf populations throughout North America. Although this approach may have many advantages over other methods, it is still crucial to recognize study-related factors that influence results and to keep these factors in mind when designing monitoring programs or comparing results of studies. The following recommendations are provided to improve future efforts to estimate wolf density via radiotelemetry:

1. Recognize the tradeoffs between the number of packs and the radiolocation effort.

Under most situations at least 6 adjacent packs should be monitored to adequately determine density. If fewer than 6 are included, recognize the need to monitor more intensively. Further, different regions of a study area can harbor different densities of wolves and these regions need to be adequately represented, increasing the number of packs to be monitored. As the number of adjacent packs drops the radiolocation effort should increase to maintain the same increase in population area with the addition of 5 locations per pack (Fig. 7).

2. Density estimates should be based on sufficient independent radiolocations/pack to minimize influences of sampling effort.

Because it can be very difficult and expensive to get an adequate sample of independent locations in a year, it probably will be necessary to combine data over years. Even with a high annual radiolocation effort of 60 locations per pack, density is still significantly influenced by radiolocation effort.

3. Maintain consistent radiolocation effort among years or evaluate differences via regression.

If density estimates are significantly correlated with radiolocation effort, then regression results may be useful to standardize density estimates to a common level of radiotracking. If radiolocation effort is variable among years, mean pack size should be considered as an alternative population index.

4. When reporting wolf densities, thoroughly describe the methods, assumptions, and radiolocation effort so others can evaluate your results.

It is important to report the number of locations/pack, the number of packs involved, and a thorough description of methods and assumptions for estimating the population area.

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APPENDIX A

Appendix A contains the SAS code for calculating home range or population areas using the 160° angle to add concavity to the population area. The program requires a good understanding of the SAS language and SAS data sets to use it properly. This SAS code is available from the author in electronic form. A good reference for learning the SAS language is Jaffe (1994).

Below is an example of the SAS code using a macro loop within a macro loop for calculating convex population areas for groups of 5 adjacent packs 100 times at each of 15 sampling intensities (from 10 to 150 locations per pack by 10s). The program is designed for UTM data in meters all from the same UTM zone. On a Pentium 166 PC this code took 25 hours to complete.

Three other programs are available. One calculates a single concave population area (similar to the example below but measures a single concave polygon one time). Another calculates the individual home range sizes as MCPs for any number of packs or individual animals. The last calculates a concave population area but one using the intersections of individual MCP lines as the corners creating concavity within the population area polygon. All can be made to plot the polygons they are measuring. Most of the code in these programs was modified from SAS code in the appendix of White and Garrott (1990), pages 343 – 349.

```

title "Concave Area Polygon Calculation, 5 packs";
options nonotes nosource;
options PS=60;

libname BURCH 'C:\denawolf\5sas';

%MACRO PACKMAC;
%DO C=1 %TO 15; *number of locations per pack x 10. Start of first Macro loop;

%MACRO WOLFMAC;
%DO L=1 %TO 100; *number of iterations for each group at each sampling level. Start of second macro loop;
%PUT # locations per pack= &C.0;
%PUT Now on iteration &L;

*****;
*This section of code randomly selects the group of packs to sample from
by using the predetermined groups of packs in the file "FiveSET";

data BURCH.PKFIVE;
    set BURCH.FIVESET;
    rand = ranuni(0);

proc sort; by rand;

data BURCH.PKFIVE1;
    x=1;
    set BURCH.PKFIVE point=x;
    output;
    stop;
run;

data BURCH.PKFIVE2;
    if _n =1 then set BURCH.PKFIVE1;
    set BURCH.WOLF2; *****INPUT DATA SET*****;
run;

data BURCH.PKFIVE3;
    set BURCH.PKFIVE2;
    where id2=pack1 |id2=pack2 |id2=pack3 |id2=pack4 |id2=pack5;
run;

*****;

data BURCH.WOLFDATA;
    set BURCH.PKFIVE3;
    rand = ranuni(0);
    dummy=1;
    keep x y id dummy rand max;

proc sort; by id rand;

data BURCH.WOLF2; * This randomly select obs from each pack;
    array pack{8100} $ 16 id1-id8100;
    array xcoor{8100} x1-x8100;
    array ycoor{8100} y1-y8100;
    retain x1-x8100 y1-y8100 id1-id8100 n;
    set BURCH.WOLFDATA; by id;
    keep x y id dummy max;
    if first.id then n=0;

n=n+1;
xcoor{n}=x; ycoor{n}=y; pack{n}=id;

```

```

if last.id then do;
  do i=1 to (&C.0); *****number of locations per pack;
    x=xcoor{i};
    y=ycoor{i};
    id=pack{i};
    output;
  end; * i loop;
end; * from last.id;

proc sort data = BURCH.WOLFDAT2; by dummy id;

data BURCH.CORNERS;
  array pack{8100} $ 16 id1-id8100;
  array xcoor{8100} x1-x8100;
  array ycoor{8100} y1-y8100;
  retain x1-x8100 y1-y8100 id1-id8100 n;
  set BURCH.WOLFDAT2; by dummy id;
  keep id x y dummy M max;
if first.dummy then n=0;
n=n+1;
if n>8100 then do;
  put 'ERROR -- More than 8100 observations for' id=;
end;
xcoor{n}=x; ycoor{n}=y; pack{n}=id;
if last.dummy then do;
  * find minimum y value;
  imin=1;
  do i=2 to n;
    if ycoor{i}<ycoor{imin} then imin=i; end;
  * put minimum y coordinate to position n+1;
  xcoor{n+1}=xcoor{imin}; ycoor{n+1}=ycoor{imin}; pack{n+1}=pack{imin};
  M=0; minangle=0;
  * Start loop to find the rest of the corners;
  do until (imin=n+1);
    M=M+1;
    temp=xcoor{M}; xcoor{M}=xcoor{imin}; xcoor{imin}=temp;
    temp=ycoor{M}; ycoor{M}=ycoor{imin}; ycoor{imin}=temp;
    tempo=pack{M}; pack{M}=pack{imin}; pack{imin}=tempo;
    imin=n+1; v=minangle; minangle=360;
    do i=M+1 to n+1;
      link thetacal;
      if theta > v then do;
        if theta < minangle then do;
          imin=i; minangle=theta;
        end;
      end;
    end;
  end;
  npoly=M;
  * Output polygon vertices to file;
  do i=1 to npoly;
    x=xcoor{i};
    y=ycoor{i};
    id=pack{i};
    output;
  end;
end; *from if last dummy;
return;

* Determin theta -- a number between 0 and 360 that is not the angle;
* made by point at M and point at i with the horizontal ;

```

* but which has the same order properties as the true angle ;

```
thetacal: dx=xcoor{i}-xcoor{M}; ax=abs(dx);
          dy=ycoor{i}-ycoor{M}; ay=abs(dy);
          if dx=0 & dy=0 then theta=0;
            else theta=dy/(ax+ay);
          if dx<0 then theta=2-theta;
            else if dy<0 then theta=4+theta;
          theta=theta*90;
return;
```

```
data BURCH.CORNER1;
  set BURCH.CORNERS;
  keep x y id dummy M max;
run;
```

*Code to find the new corners to add some concavity to the polygon:

```
data BURCH.CORNER2;
  set BURCH.CORNERS BURCH.WOLFDAT2;
  keep x y id dummy M max;
run;
```

```
data BURCH.NEWPTS;
  array pcorn{1000} $ 16 id1-id1000;
  array cornx{1000} x1-x1000;
  array corny{1000} y1-y1000;
  retain x1-x1000 y1-y1000 id1-id1000 n k h g i j f;

  array pack{9000} $ 16 id1-id9000;
  array xcoor{9000} x1-x9000;
  array ycoor{9000} y1-y9000;
  retain x1-x9000 y1-y9000 id1-id9000 n k h g i j f;
  set BURCH.CORNER2; by dummy;
  keep x y id dummy M max;
```

```
if first.dummy then do;
  n=0; k=0; h=0; g=0; i=0; j=0; f=0;
end;
```

```
n=n+1;
xcoor{n}=x; ycoor{n}=y; pack{n}=id;
```

```
if M ^= . then do;
  k=k+1;
  h=h+1;
  cornx{k}=x; corny{k}=y; pcorn{k}=id;
end;
```

```
if last.dummy then do;
```

```
  do g=1 to k;
    x=xcoor{g};
    y=ycoor{g};
    id=pack{g};
    output; *output to file BURCH.NEWPTS;
  end;
```

```
  do j=1 to k-1;
    if pcorn{j}=pcorn{j+1} then goto s100;
    do i=1 to n;
      a=((cornx{j}-xcoor{i})**2+(corny{j}-ycoor{i})**2)**0.5;
```

```

b= ((xcoor{i}-cornx{j+1})*2+(ycoor{i}-corny{j+1})*2)**0.5;
c= ((cornx{j}-cornx{j+1})*2+(corny{j}-corny{j+1})*2)**0.5;

* alpha is the angle opposite distance 'c';

if a=0 or b=0 or c=0 then alpha=0;
else
  alpha= acos((a**2+b**2-c**2)/(2*a*b));

  link radcalc;

  if alpha > rad then do;
    * output to file BURCH.NEWPTS;
    x=xcoor{i};
    y=ycoor{i};
    id=pack{i};
    output;
  end; * end of output loop;
end; *end of i loop;
s100: * from goto statement;

if j+1 = h then do; * this loop closes the polygon;

  do f=1 to n;

    a= ((cornx{1}-xcoor{f})*2+(corny{1}-ycoor{f})*2)**0.5;
    b= ((xcoor{f}-cornx{h})*2+(ycoor{f}-corny{h})*2)**0.5;
    c= ((cornx{1}-cornx{h})*2+(corny{1}-corny{h})*2)**0.5;

    if a=0 or b=0 or c=0 then alpha=0;
    else
      alpha= acos((a**2+b**2-c**2)/(2*a*b));
      if alpha > rad then do;
        * output to file BURCH.NEWPTS;
        x=xcoor{f};
        y=ycoor{f};
        id=pack{f};
        output;
      end; * end of output loop;
    end; * end of f loop;
  end; * end of j+1=h loop;
end; * end of j loop;
end; * end from if last.dummy;

radcalc:
  deg = 170;
  rad = (deg*3.141592654)/180;
return;

* code to order the final file of corner coordinates in clockwise order;

Proc means data = BURCH.NEWPTS noprint;
  var x y max;
  output out=BURCH.AV mean=xbar ybar max2;
run;

data BURCH.COMBINE1;
  set BURCH.NEWPTS BURCH.AV;
run;

data BURCH.COMBINE2;
  set BURCH.COMBINE1;

```



```

        keep x y id dummy max;
    if x = . then do;
        x = xbar;
        y = ybar;
        max = max2;
        id = 20;
        dummy = 1;
    end;
run;

data BURCH.POLYGON;
    array pack{1000} $ 16 id1-id1000;
    array xcoor{1000} x1-x1000;
    array ycoor{1000} y1-y1000;
    retain x1-x1000 y1-y1000 id1-id1000 n;
    set BURCH.COMBINE2; by dummy;
    keep x y id dummy max;

    if first.dummy then n=0;
    n=n+1;
    xcoor{n}=x; ycoor{n}=y; pack{n}=id;

    if last.dummy then do;
        xmax=1;
        do i=2 to n-1;
            if (xcoor{i} > xcoor{xmax}) & (ycoor{i} >= ycoor{n}) &
                (xcoor{i} > xcoor{n})
            then xmax=i;
        end;
        do i=1 to n-1;
            if (ycoor{i} < ycoor{xmax}) & (ycoor{i} >= ycoor{n}) &
                (xcoor{i} > xcoor{n})
            then xmax=i;
        end;

        link betacal;
        minangle=beta;
        M=0;

        do until (M=n-1);
            M=M+1;
            temp=xcoor{M}; xcoor{M}=xcoor{xmax}; xcoor{xmax}=temp;
            temp=ycoor{M}; ycoor{M}=ycoor{xmax}; ycoor{xmax}=temp;
            tempo=pack{M}; pack{M}=pack{xmax}; pack{xmax}=tempo;
            v=minangle; minangle=360;
            do i=M+1 to n-1;
                link betacal;
                if beta > v then do;
                    if beta < minangle then do;
                        xmax=i;
                        minangle=beta;
                    end; * from if beta <;
                end; * from if beta >;
            end; * end of i loop;
        end; *until loop;

        * Output polygon vertices to file;
        do i=1 to n-1;
            x=xcoor{i};
            y=ycoor{i};
            id=pack{i};
            output;
        end;
    end;
end;

```

```

    end;
end; * from if last.dummy;
return;

* Determine beta -- a number between 0 and 360 that is not the angle ;
* made by point at n (xbar ybar) and point at i with the horizontal ;
* but which has the same order properties as the true angle      ;

betacal: dx=xcoor{i}-xcoor{n}; ax=abs(dx);
        dy=ycoor{i}-ycoor{n}; ay=abs(dy);
        if dx=0 & dy=0 then beta=0;
        else beta=dy/(ax+ay);
        if dx<0 then beta=2-beta;
        else if dy<0 then beta=4+beta;
        beta=beta*90;
    return;
run;

data BURCH.WOLFAREA;
    array pack{1000} $ 16 id1-id1000;
    array xcoor{1000} x1-x1000;
    array ycoor{1000} y1-y1000;
    retain x1-x1000 y1-y1000 id1-id1000 M;
    set BURCH.POLYGON; by dummy;
    keep x y id dummy area npoly max;
if first.dummy then M=0;
M=M+1;
xcoor{M}=x; ycoor{M}=y; pack{M}=id;

if last.dummy then do;
    npoly=M;
    area=0;

    if npoly >= 3 then do;
        area=xcoor{1}*(ycoor{npoly}-ycoor{2})+
            xcoor{npoly}*(ycoor{npoly-1}-ycoor{1});
        do i=2 to npoly-1;
            area=area+xcoor{i}*(ycoor{i-1}-ycoor{i+1});
        end;
        area=area*(-0.5);
        area=(area/1000000);
    end;
end;
else area=.;
run;

data BURCH.WOLFAREA2;
    set BURCH.WOLFAREA;
    if area=. then delete;
    area=int(area);
    area=abs(area);
    perc=(area/max)*100;
    keep area perc;
    file "C:\denawolf\5sas\Five_&C.0.out" mod;
    put area perc;
run;
%END;
%MEND WOLFMAC;
%WOLFMAC

data BURCH.Five_&C.0;
    infile "C:\denawolf\5sas\Five_&C.0.out";

```

```
input area_&C.0 perc_&C.0;  
run;  
proc sort; by area_&C.0;  
run;  
%END;  
%MEND PACKMAC;  
%PACKMAC
```

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